

## Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A.

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Decomposition rates and nutrient dynamics in small-diameter woody litter (twigs, cones, and branches) were studied in four ecosystems in western Washington: high elevation Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and low elevation Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and red alder (*Alnus rubra* Bong.). Conifer twigs decomposed faster ( $k = 0.14\text{--}0.24 \text{ year}^{-1}$ ) than cones ( $k = 0.09\text{--}0.12 \text{ year}^{-1}$ ) and branches ( $k = 0.03\text{--}0.11 \text{ year}^{-1}$ ). Decomposition constants were related better to initial lignin/initial N ratios ( $r = -0.64$ ) than initial lignin concentrations. N was generally the least mobile nutrient while K was the most mobile. Many nutrients were strongly immobilized in conifer fine woody litter, including N, Mg, Mn, and Ca. There was little immobilization of N in red alder branches. N release from decomposing woody litter appears to be controlled by a critical C/N ratio. This critical C/N ratio, however, was not constant and increased as the substrate decomposition rate increased.

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L'auteur a étudié le taux de décomposition et la dynamique des éléments nutritifs de la litière ligneuse de faible diamètre (rameaux, cônes et branches) dans quatre écosystèmes de la partie ouest de l'Etat de Washington: *Abies amabilis* Dougl. à haute altitude, *Pseudotsuga menziesii* (Mirb.) Franco à faible altitude, *Tsuga heterophylla* (Raf.) Sarg., et *Alnus rubra* Bong. Les rameaux de conifères se sont décomposés plus rapidement ( $k = 0,14\text{--}0,24 \text{ an}^{-1}$ ) que les cônes ( $k = 0,09\text{--}0,12 \text{ an}^{-1}$ ) et les branches ( $k = 0,03\text{--}0,11 \text{ an}^{-1}$ ). Les constantes de décomposition étaient mieux corrélées aux ratios initiaux lignine/N ( $r = -0,64$ ) qu'aux concentrations initiales en lignine. En général, N est l'élément qui a eu le plus long temps de résidence et K le plus court. Plusieurs éléments furent fortement immobilisés dans la litière ligneuse fine de conifère, incluant N, Mg, Mn et Ca. Il s'est produit peu d'immobilisation de N dans les branches d'*Alnus rubra*. La libération de l'azote de la litière ligneuse en décomposition semble être contrôlée par un ratio critique C/N. Cependant, ce ratio critique n'était pas constant et augmentait avec l'augmentation du taux de décomposition du substrat.

[Traduit par la revue]

### Introduction

The majority of forest litter decomposition studies have involved leaves and needles. In recent years more attention has been paid to woody litter decomposition since it may play an important role in forest nutrient cycling, particularly as stands age. Fine woody litter (twigs, cones, and branches) can be a considerable proportion of litterfall (Gosz et al. 1973) and wood can account for as much as 90% of the forest floor biomass in old-growth stands (Grier and Logan 1977; Lang and Forman 1978).

Woody litter decomposition has been studied in the United States Pacific Northwest but emphasis has been on large boles (Boyce 1961; Grier 1978; Graham and Cromack 1982; Sollins 1982; Harmon et al. 1986). Nutrient dynamics in decomposing boles have also been studied (Larsen et al. 1978; Grier 1978; Lambert et al. 1980). Other than the work of Fogel and Cromack (1977), little information is available on decomposition rates and nutrient dynamics in decomposing fine woody litter in Pacific Northwest forests.

This study was conducted to determine (i) twig, cone, and branch decomposition rates in Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) ecosystems, and branch decomposition rates in a red alder (*Alnus rubra* Bong.) ecosystem; (ii) the influence of microclimate and substrate chemistry on decomposition rates of fine woody litter; and (iii) nutrient dynamics in these decomposing substrates.

### Study sites and methods

#### Study sites

The Douglas-fir (45 years old), western hemlock (70 years old), and red alder (45 years old) stands were located at the A. E. Thompson Research Center of the College of Forest Resources, University of Washington. This site is situated at an elevation of 210 m in the Cedar River watershed, approximately 50 km east of Seattle, Washington. The Pacific silver fir stand (170 years old) was located at elevation of 1150 m, near Findley Lake in the upper Cedar River watershed approximately 35 km further east. Mean annual rainfall at the Thompson site is 1440 mm with a winter maximum. At Findley Lake, mean annual precipitation is 2730 mm, mostly as snow, which persists up to 9 months. Mean annual air temperatures are 9.4 and 5.4°C at the Thompson site and Findley Lake, respectively. Soil and vegetation are described in detail in Edmonds (1982).

#### Cone, twig, and branch decomposition

Cone and twig decomposition were determined using the nylon mesh bag technique. Litterbags were 25 × 18 cm with a mesh size of 1 mm (Nylon Net Co., Tennessee). Freshly fallen female cones and twigs (10–15 mm diameter × 15 cm length) were collected in autumn 1974 from the forest floor of the three conifer stands. Cones in the Pacific silver fir ecosystem were from mountain hemlock (*Tsuga mertensiana*), a species growing in association with Pacific silver fir. Silver fir cones do not fall intact to the forest floor. Two cones weighing about 10 g total (wet weight), and a twig section weighing 10 g (dry weight) were placed in separate bags. Initial dry weights were determined for cones and twigs from moisture contents of sample cones and twigs dried to a constant weight at 75°C.

Square study plots (0.045 ha) were located in each stand in relatively flat terrain. A 5 × 5 m area was laid out in the center of each plot, and

litterbags were placed in the field in a randomized block design on November 15 (Findley Lake) and December 15 (Thompson Research Center), 1974. Three replicate litterbags were removed from the field from 3 to 72 months after placement and transported to the laboratory where contents were dried at 75°C to constant weight.

Wood discs were cut from the branches of trees in spring 1975 (Douglas-fir, western hemlock, and red alder) and summer 1975 (Pacific silver fir). Initial dry weight for each disc was determined from the moisture content of sample discs dried at 75°C to constant weight. The discs (with bark intact), 6–10 cm in diameter and 4 cm thick, were placed in the field on April 10 (Thompson Research Center) and August 20 (Findley Lake), 1985. Douglas-fir, western hemlock, and red alder branches were sampled after 12 and 25 months while Pacific silver fir branches were removed after 11, 24, 36, 48, and 63 months. Five replicates were dried to a constant weight at 75°C at each sampling time.

Mass loss at each sampling period was calculated and decomposition constants were determined according to the best fit regression method of Schlesinger and Hasey (1981).

#### Chemical analyses

All of the twigs and cones and three of the branch samples collected at each sampling time were chemically analyzed. Cones and twigs were ground in a Wiley mill to pass a No. 20 (1-mm) stainless steel mesh screen. Wedges were taken from branch samples and treated similarly. Ground material was digested using the wet oxidation method (Parkinson and Allen 1975). N and P concentrations were then determined on an autoanalyzer (Technicon Autoanalyzer II). Concentrations of K, Ca, Mg, and Mn were determined using an atomic absorption spectrophotometer (IL 353). Carbon was determined using a Leco carbon analyzer. Absolute amounts of elements at each sampling time were expressed as percentages of initial amounts. Lignin, cellulose, and acid detergent cell wall (ADCW) components for initial samples were determined using the Van Soest (1963) technique. The ADCW fraction consists of the most labile constituents, including soluble carbohydrates, soluble protein, organic acids, nonprotein nitrogen, hemicellulose, and additional soluble organic material.

#### Statistical analyses

Stepwise multiple regression analyses (SPSS) were used to determine relationships among  $k$  values and substrate chemical and microclimate variables.

## Results and discussion

#### Decomposition rates

Using the best fit regression method,  $k$  values were 0.24, 0.16, and 0.14 year<sup>-1</sup> for western hemlock, Pacific silver fir, and Douglas-fir twigs, respectively (Table 1). Different decomposition periods were involved in the calculation of  $k$ , and the  $k$  value for Douglas-fir twigs may be a low estimate since only 2 years of data were used. Mass loss of Douglas-fir and western hemlock twigs was similar after 2 years (Table 5). The best-fit regression method, however, tends to minimize errors caused by use of decomposition periods of different length.

Decomposition rates for cones were slower than those for twigs while branches had the slowest decomposition rates (Table 1). In general, western hemlock fine woody litter decomposed faster than that of Douglas-fir and Pacific silver fir.

Twig decomposition rates in this study ( $k = 0.14$ – $0.24$  year<sup>-1</sup>) were similar to those for deciduous hardwood twigs in New Hampshire ( $k = 0.11$ – $0.24$  year<sup>-1</sup>) (Gosz et al. 1973), and Vogt et al. (1983) calculated a similar  $k$  value for Pacific silver fir twigs. In drier ecosystems in the western United States cone and twig decomposition rates are slightly slower, e.g.,  $k = 0.06$ – $0.09$  year<sup>-1</sup> for twigs and  $0.05$ – $0.08$  year<sup>-1</sup> for cones in an old-growth Douglas-fir ecosystem in Oregon (Fogel and

TABLE 1. Actual and predicted  $k$  values (year<sup>-1</sup>) and 1st-year mass losses for Douglas-fir and western hemlock twigs, cones, and branches, Pacific silver fir twigs and branches, and mountain hemlock cones and red alder branches

Substrate	Actual $k^*$	Predicted $k^\dagger$	Actual 1st-year mass loss (%)	Predicted 1st-year mass loss (%) <sup>†</sup>
Douglas-fir				
Twigs	0.14	0.31	22.6	24
Cones	0.09	0.18	8.1	18
Branches	0.06	0.41	6.3	32
Western hemlock				
Twigs	0.24	0.30	19.9	22
Cones	0.10	0.19	10.1	20
Branches	0.08	0.42	9.1	30
Pacific silver fir				
Twigs	0.16	0.20	14.4	14
Branches	0.03	0.20	0.0	15
Mountain hemlock				
Cones	0.12	—	10.3	—
Red alder				
Branches	0.11	0.48	10.4	38

\*Best fit regression method of Schlesinger and Hasey (1981).

<sup>†</sup>Using Meentemeyers (1978) model based on AET and initial lignin concentration.

Cromack 1977) and  $k = 0.06$  year<sup>-1</sup> for cones in a *Pinus jeffreyi* ecosystem in Montana (Stark 1973). Fahey (1983) reported  $k = 0.15$  year<sup>-1</sup> for twigs and  $0.05$  year<sup>-1</sup> for cones in a *Pinus contorta* ecosystem in Wyoming.

$k$  values for Douglas-fir and western hemlock branches in this study were 0.06 and 0.08 year<sup>-1</sup>, respectively. These values are larger than those found for large woody boles in the Pacific Northwest. For example, Graham and Cromack (1982) and Grier (1978) found a typical  $k$  value for western hemlock logs to be 0.01 year<sup>-1</sup>, while Sollins (1982) found a  $k$  value of 0.02 year<sup>-1</sup> for Douglas-fir boles.

Douglas-fir and western hemlock branches in this study decomposed faster than similar diameter branches of the same species on the soil surface in clear-cuts in Washington;  $k = 0.01$ – $0.04$  year<sup>-1</sup> (Erickson et al. 1985; Edmonds et al. 1986). Edmonds et al. (1986) also examined red alder branch decomposition in clear-cuts and found  $k$  values ranging from 0.09 to 0.32 year<sup>-1</sup> for 8–12 cm diameter branches. This range includes the value of 0.11 year<sup>-1</sup> obtained beneath a closed canopy in this study, indicating that the clear-cutting did not influence red alder branch decomposition rate as much as it did Douglas-fir. Red alder branches in clear-cuts were much moister than Douglas-fir branches (Edmonds et al. 1986).

#### Factors controlling woody litter decomposition rates

Litter decomposition results from complex interaction among soil organisms, microclimate (temperature and moisture), litter quality (e.g., lignin and N contents), and physical properties of the litter. It is of interest to know the relative importance of these factors in the decomposition of small diameter woody litter in the study ecosystems. Many researchers have attempted to investigate relationships between these variables and to develop a unifying concept to explain and predict decomposition rates. For example, Meentemeyer (1978) has indicated that climate, as indicated by actual evapotranspiration (AET), and initial

TABLE 2. Initial percent of lignin, cellulose, and acid detergent cell wall (ADCW) components and C/N and lignin/N ratios in Douglas-fir and western hemlock cones, twigs, and branches, Pacific silver fir twigs and branches, and red alder branches

Substrate	Lignin	Cellulose	ADCW	C/N	Lignin/N
Douglas-fir					
Cones	40.9 (0.4)	39.2 (0.6)	18.5 (0.6)	311	273
Twigs	34.4 (1.9)	37.5 (2.9)	25.2 (1.7)	100	73
Branches	22.8 (0.4)	51.7 (1.3)	25.0 (1.0)	1042	570
Western hemlock					
Cones	38.1 (0.8)	40.2 (0.9)	19.7 (0.5)	104	87
Twigs	35.0 (1.9)	40.4 (1.6)	24.1 (0.6)	209	159
Branches	25.2 (0.5)	51.4 (2.6)	22.7 (3.4)	991	504
Pacific silver fir					
Twigs	36.2 (0.6)	34.4 (0.7)	28.6 (0.6)	139	106
Branches	32.8 (2.2)	38.1 (3.7)	28.9 (2.2)	680	469
Red Alder					
Branches	15.9 (1.9)	54.2 (2.1)	29.4 (0.7)	196	66

NOTE: Standard deviations are given in parentheses.

substrate lignin concentration are good predictors of decomposition rates of a variety of substrates at a macroscale level. Furthermore, he indicated that AET is several orders of magnitude better than litter quality as a predictor of decay rate.

In this study it was difficult to examine the effects of litter quality and climate separately because of the small number of data points. However, some analysis was possible. AET for the two study sites (Thompson Research Center and Findley Lake) was calculated for 1975 using the method of Thornthwaite and Mather (1955). Data were obtained from U.S. Weather Bureau stations close to the study sites at Landsburg (163 m elevation) and Stampede Pass (1206 m elevation). At Stampede Pass near Findley Lake AET was 363 mm in contrast to 511 mm at Landsburg near the Thompson Research Center. Table 1 shows actual and predicted  $k$  values and 1st-year mass loss based on AET and initial substrate lignin concentrations (shown in Table 2). Predicted  $k$  values were larger than actual for all substrates. First-year mass losses for twigs were predicted reasonably well, but predicted mass losses of cones and branches were much higher than actual.

Lignin concentrations in branches (15.9–25.2%) were much lower than those in twigs (32.8–35.0%) (Table 2), yet branches decomposed more slowly. Cones had the highest lignin concentrations (38.1–40.9%). Thus substrates low in lignin do not always decompose faster than those with high concentrations, which explains why Meentemeyer's model did not work well for branch decomposition.

Table 2 also presents cellulose and ADCW concentrations, along with C/N and lignin/N ratios for the various substrates. These data were used along with microclimate data and decomposition rates in multiple regression analyses. There was no relationship between  $k$  values and initial lignin concentrations when all substrates were considered. However, when branches were considered separately from cones and twigs, a negative relationship was observed between  $k$  and initial lignin. For branches  $r = -0.93$  ( $n = 4$ ,  $P < 0.05$ ), and for cones and twigs  $r = -0.72$  ( $n = 5$ ,  $P < 0.17$ ). Fogel and Cromack (1977) also found a relationship between  $k$  and initial lignin in Douglas-fir needles, cones, bark, and twigs (10–15 mm diam.).

This improved relationship between  $k$  and lignin was probably due to the removal of the influence of N. N concentrations

in branches were lower than those in twigs and cones. Melillo et al. (1982) attempted to combine the effects of N and lignin by relating decomposition rates to substrate initial lignin/initial N ratio. They found good relationships between decomposition rates and this ratio in hardwood leaves and in fine woody materials in a stream (Melillo et al. 1981, as cited in Melillo et al. 1982). Melillo et al. (1982) further suggested that the relationship fits a power function in the range of initial lignin/initial N ratios of 30 to 85. The range of ratios in this study was 66 to 570 where a linear function may fit better. Negative relationships between  $k$  values and initial lignin/initial N ratios ( $r = -0.64$ ,  $n = 9$ ,  $P < 0.06$ ) and initial C/N ratios ( $r = -0.61$ ,  $n = 9$ ,  $P < 0.06$ ) were observed in this study using all the data.

Differences in substrate decomposition rate could also be due to microclimate as well as substrate chemistry. Some microclimate data are available for the four stands as shown in Table 3. There are only small differences in microclimate between the three stands at the Thompson site so it is possible to examine the influence of substrate chemistry on decomposition in these stands with microclimate being relatively constant. Regression analysis indicated that  $k$  values for all substrates were best related to initial lignin/initial N ratios ( $r = -0.52$ ,  $n = 7$ ,  $P < 0.2$ ) and C/N ratios ( $r = -0.54$ ,  $n = 7$ ,  $P < 0.2$ ). Initial lignin/initial N ratio, however, only explains 25% of the variance in  $k$  at the Thompson site despite the relatively uniform microclimate among stands. Other factors must be involved. Using stepwise multiple regression analysis with all the data from both sites resulted in the following regression equation:  $k$  ( $\text{year}^{-1}$ ) =  $-8.19 - 0.0004$  initial lignin/initial N ( $r^2 = 0.40$ ) +  $0.38$  minimum litter temperature ( $^{\circ}\text{C}$ ) ( $r^2 = 0.53$ ) +  $0.08$  ADCW (%) ( $r^2 = 0.62$ ) -  $0.01$  minimum litter moisture (%) ( $r^2 = 0.64$ ) +  $0.16$  maximum litter temperature ( $^{\circ}\text{C}$ ) ( $r^2 = 0.69$ ) +  $0.07$  initial lignin (%) ( $r^2 = 0.73$ ) +  $0.07$  initial cellulose (%) ( $r^2 = 0.95$ ).

Slightly more of the variance in  $k$  across all the data (40%) could be attributed to the initial lignin/initial N ratio. The next variable to enter was minimum litter temperature, which increased the variance explained to 53%. Temperature appeared to play a more important role than moisture in these closed canopy ecosystems. Waring and Schlesinger (1985) also indi-

TABLE 3. Air and forest floor temperatures and litter moisture in red alder, Douglas-fir, western hemlock, and Pacific silver fir ecosystems, November – 1974–December 1976 (from Edmonds 1980)

Ecosystem	Air temperature, °C			Forest floor temperature, °C		Litter moisture, %*	
	Average annual	Max.	Min.	Max.	Min.	Average annual	Min.
Red alder	9.6	34.0	– 6.0	16.1	–1.7	74	57
Douglas-fir	8.0	29.0	– 6.0	17.2	–2.2	65	36
Western hemlock	9.5	30.0	– 7.0	18.3	–2.8	66	32
Pacific silver fir	5.8	27.0	–17.0	16.0	–2.0	65	39

\*Net weight basis.

cated that temperature is of primary importance. Minimum litter moisture, however, did enter the equation. In clear-cuts moisture is likely to play a more important role in the decomposition of small-diameter wood (Erickson et al. 1985; Edmonds et al. 1986). Boddy (1983), however, points out that it is difficult to separate influence of temperature and moisture in wood decomposition since they interact. Substrate moisture and temperature were not followed in this study. Altogether 7 of the 12 independent variables entered the equation explaining 95% of the variance in  $k$ . Seventy-six percent of the variance in  $k$  was explained by litter quality variables while only 19% was explained by microclimate variables.

Physical attributes of woody substrates also affect the decomposition process and must explain to some extent why branches and cones decompose slower than twigs. Physical contact with the forest floor is much less with branches and cones than with twigs, and this would tend to slow decomposition. Erickson et al. (1985) and Edmonds et al. (1986) noted that suspended wood in a clear-cut decomposed slower than wood on the soil surface. Fogel and Cromack (1977) also indicated that surface to volume ratio becomes important in wood decay as particle size increases.

#### Nutrient dynamics

Nutrient dynamics in large woody litter, i.e., logs, has received attention in the Pacific Northwest (Grier 1978; Graham and Cromack 1982). Grier (1978) indicated that N may be immobilized for as long as 25 years in decaying western hemlock logs and that Ca, Mg, and Na were also immobilized. Little attention, however, has been paid to nutrient dynamics in smaller woody substrates.

Initial N concentrations in twigs were relatively high. Highest concentrations occurred in Douglas-fir twigs (0.47%) and lowest in western hemlock twigs (0.22%, Table 4). N concentrations in twigs increased during the decomposition period. After 70 months in western hemlock twigs and 72 months in Pacific silver fir twigs, N concentrations had increased from 0.22 to 0.87% and 0.34 to 0.72%, respectively. Concentrations of P, K, and Ca in twigs dropped during the 1st year and then tended to increase as the decomposition period increased. On the other hand, concentrations of Mg and Mn changed little (Table 4). Gosz et al. (1973) found decreases of nutrients other than N during the 1st year of decomposition of yellow birch, sugar maple, and beech twigs. Fahey (1983) also noted that concentrations of P, K, Ca, and Mg in decomposing wood changed little or decreased initially then increased as decomposition proceeded.

N concentrations in conifer branches were low (0.04 to

0.07%) and increased with time (Table 5). In red alder branches N concentrations decreased in the 1st year from 0.24 to 0.19% and then increased to 0.26% after 25 months (Table 5). Concentrations of the other elements in branches generally either did not change or decreased slightly with time. In general, elemental concentrations in branches were lower than those in twigs and cones.

Concentrations of N in cones were similar to those in twigs but were slightly higher in western hemlock (0.44%) and slightly lower in Douglas-fir (0.15%) (Table 6). N concentrations increased with time and reached a maximum of 1.33% in mountain hemlock cones after 72 months. Concentrations of P, K, Mg, and Mn were similar to those in twigs, but Ca concentrations were considerably lower. During the 1st year of decomposition concentrations of these elements in cones tended to decrease and then increased slightly with the exception of Mn which continually increased (Table 6).

Although nutrient dynamics are somewhat reflected by concentrations, a better picture of immobilization or release of elements is obtained by examining changes in absolute levels over time. N and P in Douglas-fir twigs appeared to be immobilized in the 12- to 24-month period (Fig. 1a), after an initial decrease. Mg appeared to be strongly immobilized during the initial phases of decomposition of Douglas-fir twigs (Fig. 1b), but other elements were not immobilized. In western hemlock twigs, N was immobilized for 2 years and then began to be released (Fig. 2a). Mg also was strongly immobilized, as was Mn (Fig. 2b). P appeared to be immobilized between years 1 and 2 as it was in Douglas-fir twigs, but it was subsequently rapidly released (Fig. 2a). Only N was immobilized in Pacific silver fir twigs with net release occurring in the 2- to 6-year period (Figs. 3a and 3b).

N was immobilized in conifer branches (Figs. 4a, 5a, and 6a). In Pacific silver fir branches, five elements (N, P, Mn, Mg, and Ca) were immobilized at some stage during the decomposition process, with Mn being more strongly immobilized than N (Figs. 6a and 6b). Ca was also fairly strongly immobilized in western hemlock branches (Fig. 5b). No elements were immobilized in red alder branches (Figs. 7a and 7b) with the exception, perhaps, of N, which increased from 71 to 87% of initial N weight remaining in the 12- to 25-month period, suggesting slight immobilization.

Twigs and branches did not always show the same immobilization and release pattern. For example, Mg was immobilized in Douglas-fir twigs but not in branches, while Mn was immobilized in branches but not in twigs (Figs. 1b and 4b). Mn was immobilized in western hemlock twigs (Fig. 2b) and branches (Fig. 5b).

TABLE 4. Dry weights (mass) and nutrient concentrations ( $\pm$  SD) of Douglas-fir, western hemlock, and Pacific silver fir twigs in relation to duration of decomposition

Collection date*	Ecosystem	Duration of decomposition (months)	Mass (g)	% C	% N	C/N	Concentration ( $\mu\text{g/g}$ )				
							P	K	Ca	Mg	Mn
11.15.74	Pacific silver fir	0	10.0	47.2	0.34	139	410	520	4470	360	410
12.15.74	Douglas-fir	0	10.0	47.0	0.47	100	490	420	4770	210	410
	Western hemlock	0	10.0	45.9	0.22	209	530	410	2880	130	270
3.14.75	Douglas-fir	3	8.92 (0.06)	46.2 (0.4)	0.44 (0.02)	105	381 (43)	—	3581 (6)	345 (36)	281 (12)
	Western hemlock	3	9.30 (0.37)	45.5 (0.2)	0.32 (0.07)	142	304 (117)	—	2704 (191)	296 (106)	489 (202)
4.24.75	Pacific silver fir	5	8.44 (0.11)	46.8†	0.33	141	160	254	3713	228	212
6.30.75	Douglas-fir	7.5	8.24 (0.21)	48.3 (0.2)	0.50 (0.0)	97	336 (6)	277 (33)	4133 (1228)	358 (5)	215 (6)
	Western hemlock	7.5	8.36 (0.03)	47.3 (0.0)	0.46 (0.06)	103	335 (42)	385 (43)	2804 (696)	360 (40)	532 (139)
8.20.75	Pacific silver fir	9	8.90 (0.07)	51.4 (0.9)	0.44 (0.08)	117	351 (58)	168 (55)	4880 (584)	279 (79)	414 (26)
12.17.75	Douglas-fir	12	7.74 (0.16)	48.9 (1.1)	0.50 (0.05)	98	346 (33)	324 (44)	5617 (641)	368 (18)	237 (36)
	Western hemlock	12	8.01 (0.07)	47.5 (1.0)	0.42 (0.07)	113	280 (26)	313 (24)	2468 (357)	274 (19)	394 (19)
11.19.76	Pacific silver fir	24	7.89 (0.22)	52.4 (1.3)	0.52 (0.08)	101	414 (90)	277 (74)	4788 (535)	273 (35)	338 (17)
12.16.76	Douglas-fir	24	7.34 (0.26)	48.9 (0.4)	0.70 (0.04)	70	540 (39)	—	5201 (467)	342 (41)	322 (12)
	Western hemlock	24	7.54 (0.32)	47.7 (0.3)	0.66 (0.08)	73	507 (63)	—	2966 (236)	316 (39)	576 (95)
10. 8.80	Western hemlock	70	2.42‡	47.7	0.87	57	576	490	5087	381	537
11.18.80	Pacific silver fir	72	3.77 (2.06)	47.8†	0.72	69	476	594	5081	298	302

\*Month, day, year.

†Only one sample analyzed.

‡Only one sample collected.

TABLE 5. Dry weights (mass) and nutrient concentrations ( $\pm$ SD) of Douglas-fir, western hemlock, Pacific silver fir, and red alder branches in relation to duration of decomposition

Collection date*	Ecosystem	Duration of decomposition (months)	Mass (g)	% C	% N	C/N	Concentration ( $\mu\text{g/g}$ )				
							P	K	Ca	Mg	Mn
4.10.75	Douglas-fir	0	100†	46.3 (0.3)	0.04 (0.0)	1042	105 (1)	295 (2)	385 (1)	67 (3)	48 (1)
	Western hemlock	0	100	46.5 (0.5)	0.05 (0.0)	991	110 (4)	332 (3)	533 (4)	92 (3)	155 (0.5)
	Red alder	0	100	46.8 (0.4)	0.24 (0.01)	196	195 (6)	405 (8)	669 (3)	199 (1)	24 (0.3)
8.20.75	Pacific silver fir	0	100	47.8 (0.4)	0.07 (0.01)	680	81 (10)	409 (103)	1028 (1)	140 (2)	38 (0.3)
4.26.76	Douglas-fir	12	93.7 (2.4)	46.5 (0.1)	0.07 (0.01)	731	95 (20)	116 (45)	392 (162)	73 (7)	64 (16)
4.26.76	Western hemlock	12	90.9 (3.3)	46.7 (0.2)	0.06 (0.01)	810	78 (8)	259 (89)	770 (123)	93 (1)	214 (7)
4.26.76	Red alder	12	89.6 (4.7)	46.6 (0.1)	0.19 (0.03)	248	172 (87)	288 (645)	699 (123)	215 (19)	22 (4)
7. 9.76	Pacific silver fir	11	103.7 (4.6)	47.5 (0.2)	0.06 (0.01)	714	78 (11)	56 (21)	772 (131)	153 (8)	51 (1)
5.25.77	Douglas-fir	25	88.7 (7.4)	46.2 (0.6)	0.08 (0.02)	643	101 (21)	189 (67)	326 (100)	76 (19)	102 (101)
5.25.77	Western hemlock	25	85.5 (5.1)	46.4 (0.7)	0.08 (0.03)	619	133 (76)	162 (76)	927 (451)	112 (53)	315 (95)
5.25.77	Red alder	25	80.0 (4.6)	46.5 (0.5)	0.26 (0.04)	184	164 (13)	375 (173)	834 (89)	182 (31)	10 (9)
8.30.77	Pacific silver fir	24	105.8 (5.7)	46.8 (0.1)	0.11 (0.02)	455	62 (52)	128 (53)	1099 (31)	150 (13)	72 (12)
8.28.78	Pacific silver fir	36	96.9 (2.4)	46.3 (0.2)	0.09 (0.01)	540	120 (48)	97 (51)	1101 (165)	134 (31)	73 (18)
8.15.79	Pacific silver fir	48	92.7 (5.3)	46.4 (0.5)	0.11 (0.02)	430	78 (56)	162 (37)	1113 (169)	121 (24)	70 (7)
11.18.80	Pacific silver fir	63	85.0 (0.3)	46.6 (0.4)	0.12 (0.03)	399	76 (59)	185 (86)	1108 (95)	112 (6)	85 (5)

\*Month, day, year.

†Normalized to 100 g since different starting weights were used (includes bark weight).

TABLE 6. Dry weights (mass) and nutrient concentrations ( $\pm$ SD) of Douglas-fir, western hemlock, and mountain hemlock\* cones in relation to duration of decomposition

Collection date*	Ecosystem	Duration of decomposition (months)	Mass (g)	% C	% N	C/N	Concentration ( $\mu\text{g/g}$ )				
							P	K	Ca	Mg	Mn
11.15.74	Pacific silver fir	0	10‡	47.0	0.40	118	410	350	1420	260	60
12.15.74	Douglas-fir	0	10‡	46.7	0.15	311	440	810	1170	520	90
	Western hemlock	0	10‡	45.8	0.44	104	760	450	1040	270	380
3.14.75	Douglas-fir	3	9.96 (0.19)	44.0 (0.4)	0.22 (0.02)	200	330 (169)	175 (47)	1044 (95)	487 (45)	202 (55)
	Western hemlock	3	9.65 (0.42)	44.8 (0.4)	0.38 (0.02)	118	310 (34)	322 (46)	1113 (67)	280 (11)	391 (30)
6.30.75	Douglas-fir	6	9.46 (0.17)	46.3 (0.7)	0.27 (0.04)	171	167 (9)	384 (177)	742 (41)	365 (110)	124 (27)
	Western hemlock	6	9.52 (0.21)	46.0 (0.7)	0.44 (0.02)	105	250 (20)	498 (116)	1115 (112)	239 (9)	321 (16)
8.20.75	Pacific silver fir	9	9.27 (1.06)	47.2 (0.4)	0.51 (0.0)	93	376 (78)	136 (37)	1246 (495)	193 (42)	130 (43)
12.17.75	Douglas-fir	12	9.19 (0.58)	46.8 (0.4)	0.30 (0.11)	156	177 (79)	360 (83)	1178 (1)	462 (49)	140 (13)
	Western hemlock	12	8.99§	47.5	0.40	119	233	336	1031	247	278
1. 8.76	Pacific silver fir	14	8.97 (0.60)	46.1 (0.4)	0.42 (0.11)	110	285 (70)	315 (100)	1227 (250)	184 (48)	135 (50)
11.19.76	Pacific silver fir	24	8.31 (0.25)	48.6 (0.4)	0.81 (0.12)	60	581 (68)	408 (222)	1739 (444)	304 (53)	229 (176)
11.18.80	Pacific silver fir	72	6.15 (0.71)	45.1 (0.5)	1.33 (0.18)	34	789 (139)	681 (83)	2174 (960)	334 (13)	307 (185)

\*Mountain hemlock cones in Pacific silver fir ecosystem.

†Month, day, year.

‡Normalized to 10 g since different starting weights were used.

§Only one sample collected.

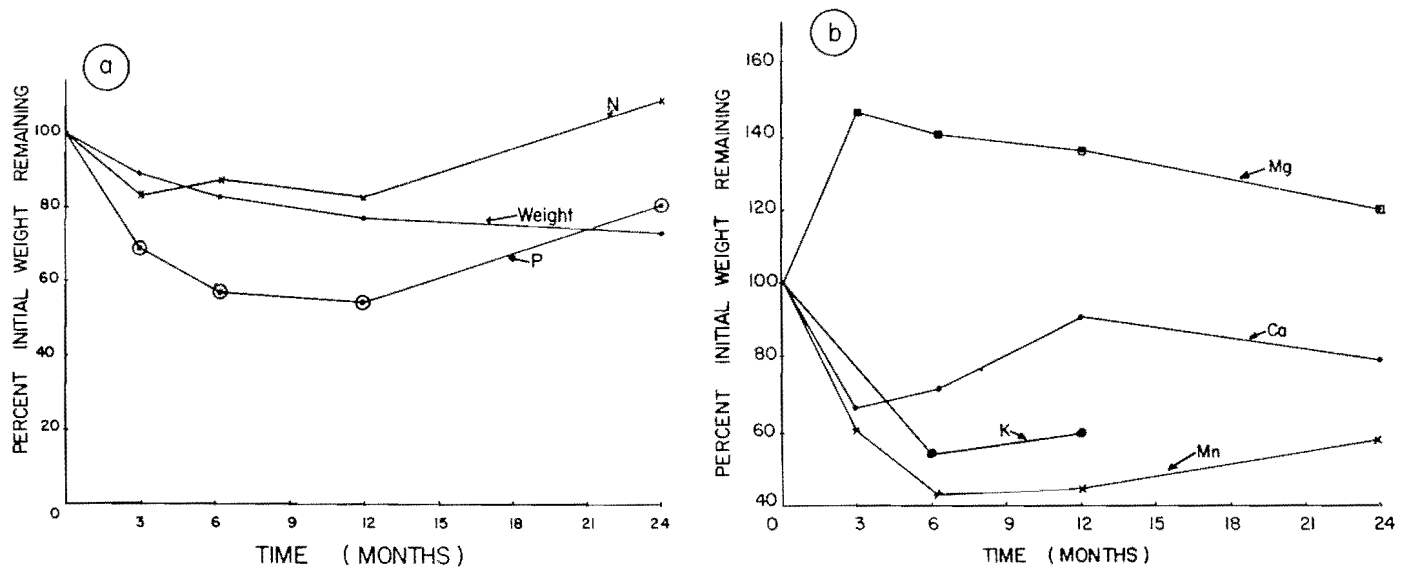


FIG. 1. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing Douglas-fir twigs in relation to time.

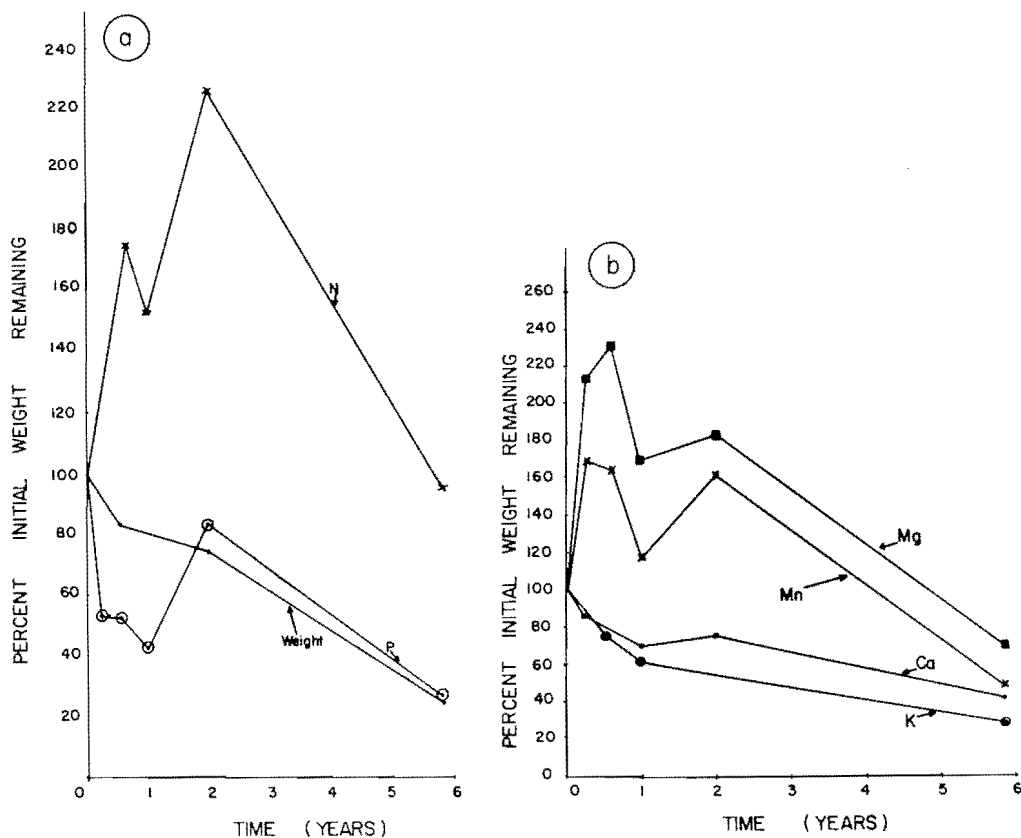


FIG. 2. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing western hemlock twigs in relation to time.

N and Mn were strongly immobilized in Douglas-fir (Fig. 8a) and mountain hemlock (Fig. 8c) cones but not in western hemlock cones (Fig. 8b). P was also immobilized in mountain hemlock cones between 2 and 6 years (Fig. 8c).

In general, N was the least mobile element and K the most mobile. However, in conifer branches and mountain hemlock cones, Mn was less mobile than N. On the other hand, Mn was

the most mobile element in red alder branches. P, Ca, and Mg generally had intermediate mobility.

Critical C/element ratios have been suggested as controls of the immobilization and release of nutrient elements in decomposing substrates. Mineralization of N from litter has traditionally been related to the C/N ratio. Lutz and Chandler (1946) suggest that N mineralization should occur at C/N ratios

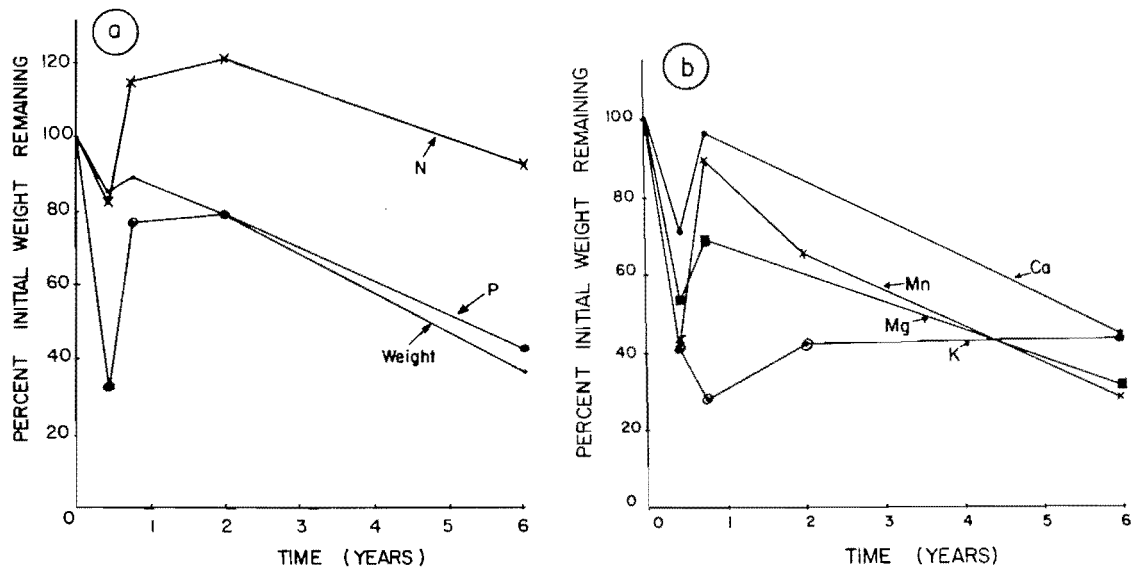


FIG. 3. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing Pacific silver fir twigs in relation to time.

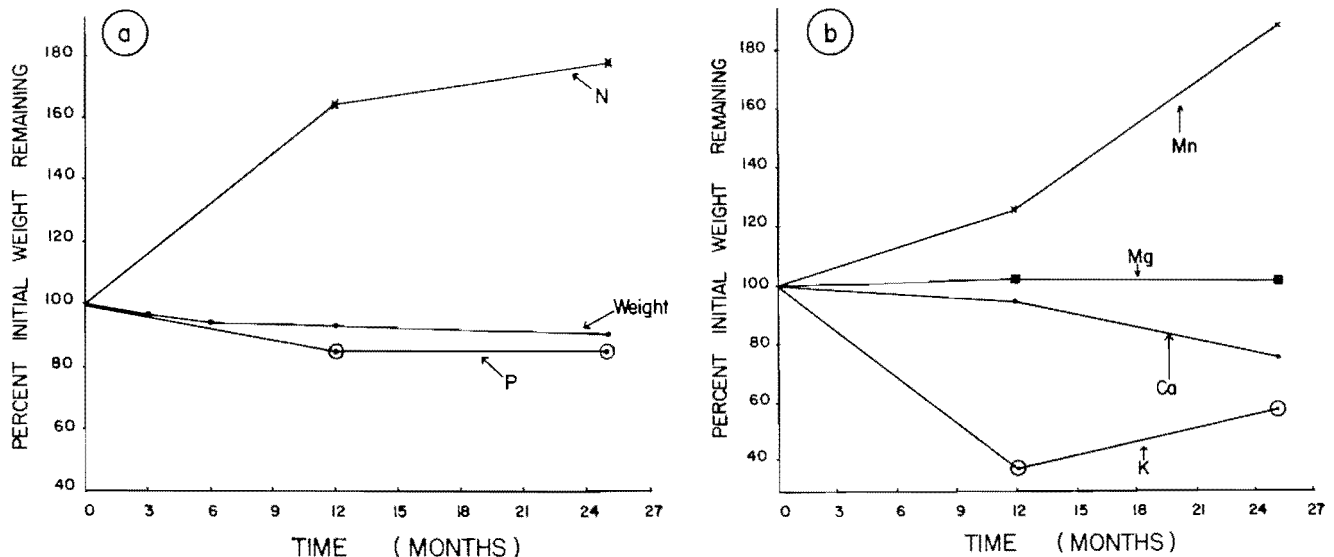


FIG. 4. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing Douglas-fir branches in relation to time.

between 20/1 and 30/1. This appears to be the case for decomposing needle and leaf litter in the ecosystems studied (Edmonds 1980, 1984), but it does not appear to be the case for woody substrates. Critical C/N ratios for N mineralization appear to be greater than 100/1 for twigs and branches. For example, release of N occurred in western hemlock twigs when the C/N ratio fell from 113 to 57 (Fig. 2a, Table 4) and from 101 to 69 in Pacific silver fir twigs (Fig. 3a, Table 4). Cones tended to behave similarly to twigs with a critical C/N ratio for release near 100 (Fig. 8, Table 6). Gosz et al. (1973) also found that N was released from deciduous hardwood twigs at high C/N ratios.

In Pacific silver fir branches the C/N ratio had only fallen to 399 after 5 years of decomposition (Table 5) and N was still strongly immobilized (Fig. 6a). No N release was observed in Douglas-fir and hemlock branches where C/N ratios were still greater than 600 after 2 years of decomposition. In red alder branches, however, N appeared initially to be released (Fig. 7a)

even though the initial C/N ratio was 196 (Table 5). Nitrogen immobilization appeared to be occurring in the 12- to 24-month period when the C/N ratio increased to more than 200 (Table 6). Thus the critical C/N ratio for N release in branches appears to be higher than that for twigs (nearly 200 for red alder branches). No N release was observed from conifer branches during this study because the C/N ratios in these substrates apparently had not fallen to a critical level. Larger woody substrates may have an even higher critical C/N ratio than branches. For example, using data from Grier (1978), N release commenced at a C/N ratio of about 370 in western hemlock logs.

The above discussion indicates that there is no fixed critical C/N ratio for release of N from decomposing substrates. Rather, the critical C/N ratio for N release is related to substrate decomposition rate. This concept has been proposed by Berg and Staaf (1981), Bosatta and Staaf (1982), and Bosatta and Ågren (1985) and is illustrated by the data in Fig. 9 for a variety of leaf, needle, and woody substrates. As the decomposition



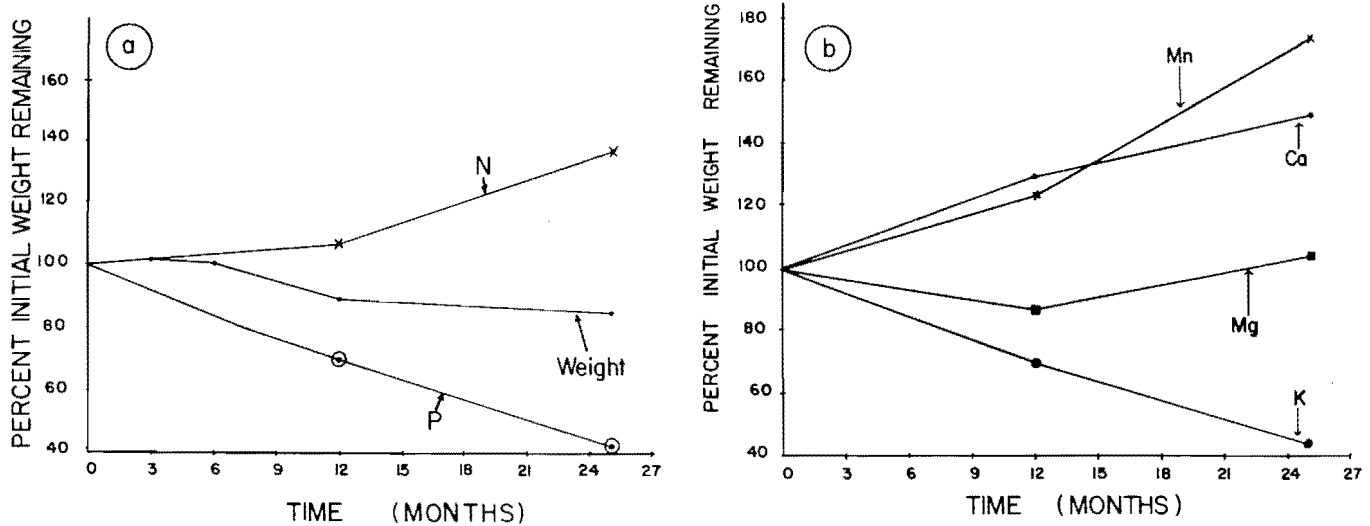


FIG. 5. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing western hemlock branches in relation to time.

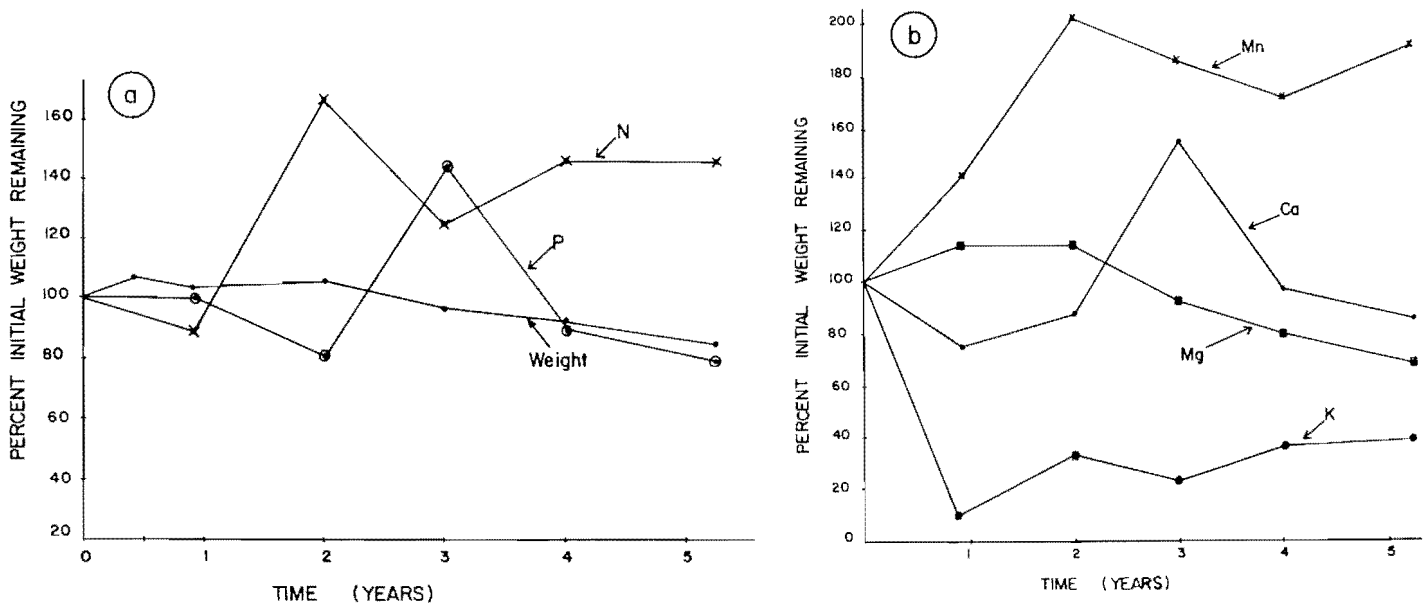


FIG. 6. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing Pacific silver fir branches in relation to time.

rate decreases the critical C/N ratio for release increases, and while it may be near 30 for needles and leaves, it is greater than 100 for twigs and more than 300 for conifer branches and logs.

The marked difference in the critical C/N ratio from needles to woody substrates may be due to the fact that microbes decomposing needles are different from wood decomposing organisms. Wood decomposers are generally able to exist on lower levels of N (Cowling and Merrill 1966) and thus may release N at higher C/N ratios. On the other hand, only the bulk C/N ratio in wood was determined in this study and at microsites near fungi and bacteria the C/N ratio may be lower.

Critical C/P ratios have also been suggested to be important for P release. Lousier and Parkinson (1978) suggested a critical C/P ratio of 230 for P release in aspen litter. Edmonds (1980), however, found that P was released from needles and leaves in the study ecosystems at much higher C/P ratios (1672). P was not generally immobilized in twigs and cones but it was immobilized in Pacific silver fir branches (Fig. 6a) and

mountain hemlock cones (Fig. 8c). The critical C/P for P release for these substrates appears to be near 6000, considerably higher than that suggested by Lousier and Parkinson (1978). Grier (1978) noted no P immobilization in western hemlock logs with initial C/P ratios of 2770. Furthermore, Gosz et al. (1973) did not observe P immobilization in twigs with initial C/P ratios near 1000. Thus woody tissues seem to have much higher critical C/P ratios for P release than that for foliage.

In contrast to P, Mg was strongly immobilized in Douglas-fir twigs (Fig. 1b) and branches (Fig. 4b) and in western hemlock twigs (Fig. 2b). A critical C/Mg ratio of about 1500 appears to operate for twigs and cones but no clear ratio occurred for branches. Mg was also strongly immobilized in western hemlock logs where initial C/Mg ratios averaged 3571 (Grier 1978) and release began when the C/Mg ratio fell to 1190. Mg was not immobilized in birch, maple, and beech twigs, with initial C/Mg ratios less than 1000 (Gosz et al. 1973).

Mn was also strongly immobilized, particularly in branches.

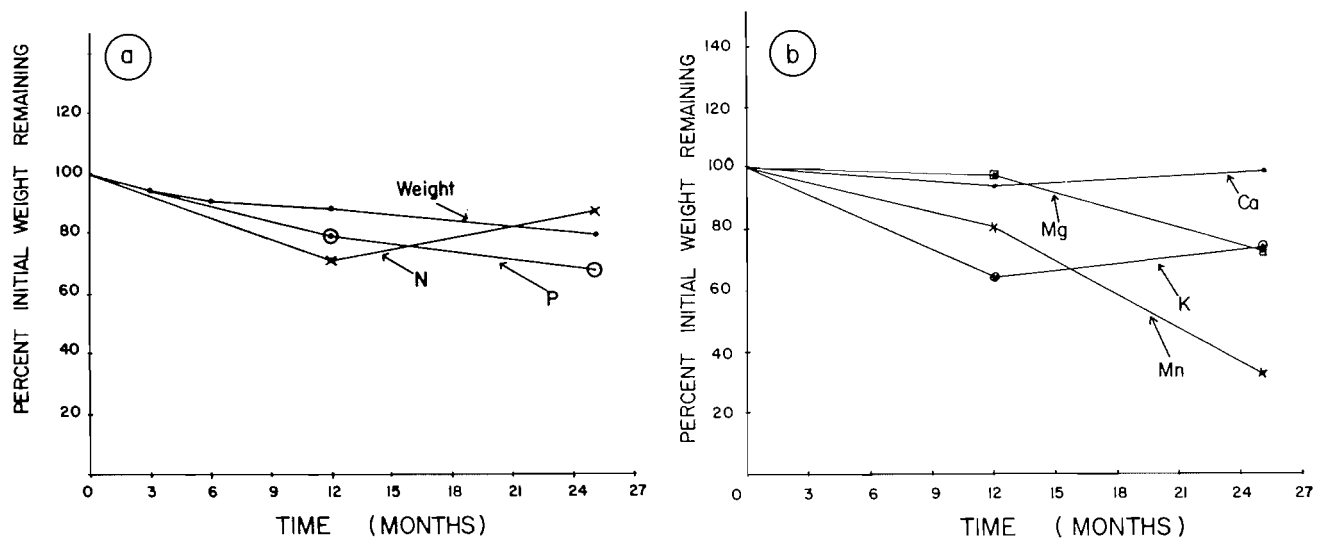


FIG. 7. Percent of initial weight remaining of (a) N, P, and mass (dry weight) and (b) K, Mg, Ca, and Mn in decomposing red alder branches in relation to time.

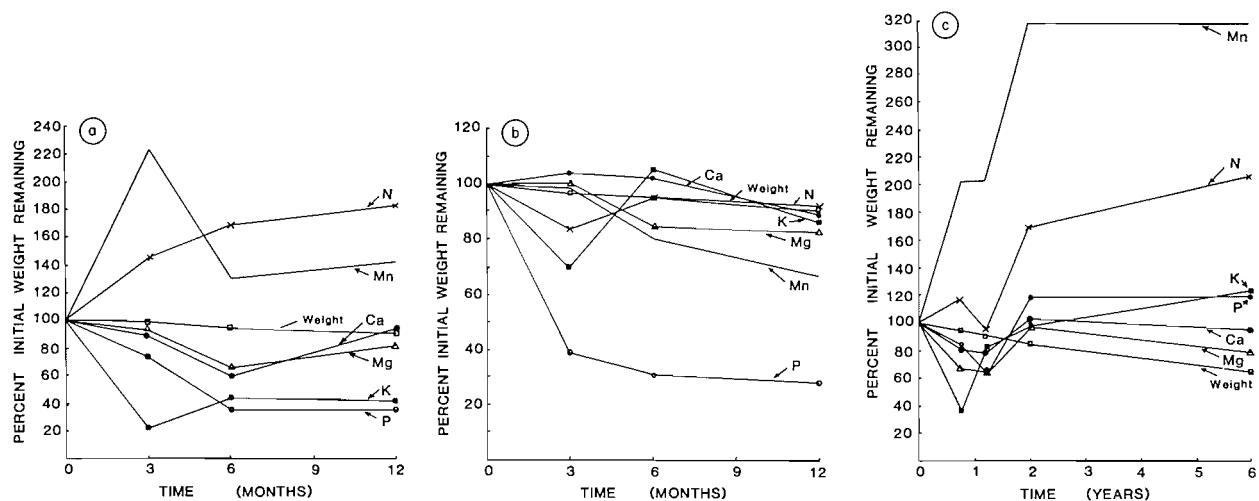


FIG. 8. Percent of initial weight remaining of N, P, K, Mg, Mn and mass (dry weight) in decomposing (a) Douglas-fir, (b) western hemlock, and (c) mountain hemlock cones in relation to time.

In some cases it was even less mobile than N (e.g., in Pacific silver cones and branches and Douglas-fir and western hemlock branches, Table 8). A critical C/Mn ratio for release appeared to be near 1700/1 in twigs. Gosz et al. (1973) observed no net Mn immobilization in twigs with initial C/Mn ratios less than 1000/1.

Ca was immobilized in western hemlock branches (Fig. 5b) and cones (Fig. 8b) and Pacific silver fir branches (Fig. 6b). Grier (1978) also noted that Ca was immobilized in western hemlock logs and using his data a critical C/Ca for release is greater than 200. This seems to be near the critical value for Ca immobilization in this study. Gosz et al. (1973) noted no Ca immobilization in twigs with initial C/Ca ratios less than 100. K was generally the most mobile element in woody substrates as it was in needles and leaves in these ecosystems (Edmonds 1980), although occasionally P, Mg, and Mn were more mobile than K.

## Conclusions

The major findings of this study were the following: (i) Conifer twigs decomposed faster than cones and branches. (ii) Decomposition constants ( $k$  values) for all woody substrates were better related to initial lignin/initial N ratios ( $r = -0.64$ ) than to initial lignin concentration. More variance in  $k$  was explained by litter quality variables than by temperature and moisture. (iii) N was generally the least mobile nutrient, while K was the most mobile. Many nutrients were strongly immobilized in decomposing conifer fine woody litter, including N, Mg, Mn and Ca, which is in contrast with immobilization patterns in conifer needles where only N was immobilized. No elements were immobilized in red alder branches. The critical C/N ratio for N release was not constant and was related to substrate decomposition rate. It was  $> 100/1$  for twigs and cones and  $> 300/1$  for branches and logs.

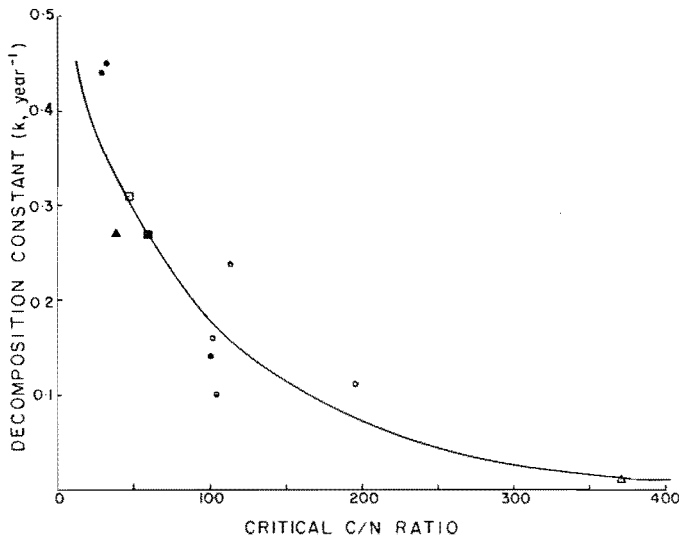


FIG. 9. Decomposition constants ( $k$ ) for Douglas-fir and red alder leaves (●; Edmonds 1980), hardwood twigs (■; Gosz et al. 1973), Radiata pine needles (▲; Will 1967), Scots pine needles (□; Berg et al. 1982), red alder branches, hemlock cones, and Douglas-fir, western hemlock, and Pacific silver fir twigs (○; this study) and western hemlock logs (△; Grier 1978) in relation to the critical C/N ratio for N release.  $k = 0.49e^{-0.01C/N}$  ( $r^2 = 0.92$ ).

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- BODDY, L. 1983. Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. *Soil Biol. Biochem.* **15**: 149–157.
- BOYCE, J. S. 1961. *Forestry pathology*. McGraw-Hill, New York.
- BERG, B., and STAAF, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. *Eco. Bull.* **33**: 163–178.
- BERG, B., HANNUS, K., POPOFF, T., and THEANDER, O. 1982. Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. *I. Can. J. Bot.* **60**: 1310–1319.
- BOSATTA, E., and ÅGREN, G. I. 1985. Theoretical analysis of decomposition of heterogeneous substrates. *Soil. Biol. Biochem.* **17**: 601–610.
- BOSATTA, E., and STAAF, H. 1982. The control of nitrogen turn-over in forest litter. *Oikos*, **39**: 143–151.
- COWLING, E. B., and MERRILL, W. 1966. Nitrogen in wood and its role in wood deterioration. *Can. J. Bot.* **44**: 1539–1554.
- EDMONDS, R. L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. *Can. J. For. Res.* **10**: 327–337.
- . 1982. Introduction. In *Analysis of coniferous forest ecosystems in the western United States*. Edited by R. L. Edmonds. IBP Synthesis Series No. 10. Dowden, Hutchinson and Ross, Stroudsburg, PA. pp. 1–27.
- . 1984. Long-term decomposition and nutrient dynamics in Pacific silver fir needles in western Washington. *Can. J. For. Res.* **14**: 395–400.
- EDMONDS, R. L., VOGT, D. J., SANDBERG, D. H., and DRIVER, C. H. 1986. Decomposition of Douglas-fir and red alder wood in clear-cuts. *Can. J. For. Res.* **16**: 822–831.
- ERICKSON, H. E., EDMONDS, R. L., and PETERSEN, C. E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir and ponderosa pine ecosystems. *Can. J. For. Res.* **15**: 914–921.
- FAHEY, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* spp. latifolia) ecosystems, south-eastern Wyoming. *Ecol. Monogr.* **53**: 51–72.
- FOGEL, R., and CROMACK, K., JR. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. *Can. J. Bot.* **55**: 1632–1640.
- GOSZ, J. R., LIKENS, G. E., and BORMANN, F. H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. *Ecol. Monogr.* **43**: 173–191.
- GRAHAM, R. L., and CROMACK, K., JR. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* **12**: 511–521.
- GRIER, C. C. 1978. A *Tsuga heterophylla* – *Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Can. J. For. Res.* **8**: 198–206.
- GRIER, C. C., and LOGAN, R. S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**: 373–400.
- HARMON, M. E., FRANKLIN, J. F., SWANSON, F. J., SOLLINS, P., GREGORY, S. V., LATTIN, J. D., ANDERSON, N. H., CLINE, S. P., AUMEN, N. G., SEDELL, J. R., LIENKAEMPER, G. W., CROMACK, K., JR., and CUMMINS, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302.
- LAMBERT, R. L., LANG, G. E., and REINERS, W. A. 1980. Loss of mass and chemical change in decaying boles of a subalpine fir forest. *Ecology*, **61**: 1460–1473.
- LANG, G. E., and FORMAN, R. T. T. 1978. Detritus dynamics in a mature oak forest: Huteson Memorial Forest, New Jersey. *Ecology*, **59**: 580–595.
- LARSEN, M. J., JURGENSEN, M. F., and HARVEY, A. E. 1978. Dinitrogen fixation associated with the activities of some common wood decay fungi in western Montana. *Can. J. For. Res.* **8**: 341–345.
- LOUSIER, J. D., and PARKINSON, D. 1978. Chemical element dynamics in decomposing leaf litter. *Can. J. Bot.* **56**: 2795–2812.
- LUTZ, H. J., and CHANDLER, R. F. 1946. *Forest soils*. John Wiley and Sons, New York.
- MELILLO, J. M., NAIMAN, R. J., and ABER, J. D. 1981. Wood decomposition dynamics as a function of quality of material and stream order in Quebec. In *The Matamek Research Program Annual Report for 1980*. Edited by R. J. Naiman. WHOI-81-49.
- MELILLO, J. M., ABER, J. D., and MURATORE, J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**: 621–626.
- MEENTEMEYER, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**: 465–472.
- PARKINSON, J. A., and ALLEN, S. E. 1975. A wet oxidation procedure for the determination of nitrogen and mineral elements in biological materials. *Commun. Soil Sci. Plant Anal.* **6**: 1–11.
- SCHLESINGER, W. H., and HASEY, M. M. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology*, **62**: 762–774.
- SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* **12**: 18–28.
- STARK, N. 1973. Nutrient cycling in a Jeffrey pine forest ecosystem. Institute of Microbiology, University of Montana, Missoula.
- THORNTWHAITE, C. W., and MATHER, J. R. 1955. The water balance. *Publ. Climatol.* **8**: 1–104.
- VAN SOEST, P. J. 1963. Use of detergents in the analysis of fibrous feeds II. A rapid method for determination of fiber and lignin. *J. Assoc. Off. Anal. Chem.* **49**: 546–551.
- VOGT, K. A., GRIER, C. C., MEIER, C. E., and KEYES, M. R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington as affected by fine root input. *Ecol. Monogr.* **53**: 139–159.
- WARING, R. H., and SCHLESINGER, W. H. 1985. *Forest ecosystems—concepts and management*. Academic Press, New York.
- WILL, G. 1967. Decomposition of *Pinus radiata* litter on the forest floor. Part 1. Changes in dry matter and nutrient content. *N.Z. J. Sci.* **10**: 1030–1044.